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Complex In-Substrate Dinosaur (Sauropoda, Ornithopoda) Foot Pathways Revealed by Deep Natural Track Casts from the Lower Cretaceous Xiagou and Zhonggou Formations, Gansu Province, China

Lida Xing[a], Daniel Marty[b], Hailu You[c], Daqing Li[d], Hendrik Klein[e], Dirk Knaust[f], Jianping Zhang[a], Richard T. McCrea[g], and W. Scott Persons IV[h]

[a]School of the Earth Sciences and Resources, China University of Geosciences, Beijing, China; [b]Naturhistorisches Museum Basel, Basel, Switzerland; [c]Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; [d]Gansu Agriculture University, Lanzhou, China; [e]Saurierwelt Paläontologisches Museum, Neumarkt, Germany; [f]Statoil ASA, Stavanger, Norway; [g]Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia, Canada; [h]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

ABSTRACT
Several new Early Cretaceous tracksites from the Lower Cretaceous Xiagou Formation of Gansu Province (China) with tracks of large sauropods and ornithopods are described. Previously reported bird tracks were missing due to human negligence. The studied specimens are preserved as impressions and shallow and deep natural track casts. These dinosaur tracks are first reported from the Jiuquan area in the Changma Basin, matching well with the skeletal record of diverse non-avian dinosaur-bird faunas of this region. Moreover, they add new data to the dinosaur ichnofaunas of the Lanzhou-Minhe Basin (Gansu Province) and indicate a wide distribution of dinosaur-bird assemblages in the Early Cretaceous. Regarding morphology, sauropod, and ornithopod tracks from the Lanzhou-Minhe Basin and the Jiuquan area are very similar to each other. Titanosauriform trackmakers are assumed for the sauropod tracks and possibly iguanodontids have left the large, tridactyl ornithopod tracks. Of particular interest are well-preserved, deep natural track casts of large ornithopods and sauropods preserving ridges and grooves as well as striation marks on the lateral sides of the casts that allow the reconstruction of complex pathways of the foot within the substrate. One particular sauropod *pes–manus* track cast even indicates lateral and vertical sliding within the sediment because of the presence of "double impressions of digits" on the bottom.

KEYWORDS
Dinosaur track; Natural track cast; Track formation; Foot locomotor dynamics; Ornithopoda; Sauropoda

Introduction

In the last ten years, a number of new non-avian dinosaur and bird fossil discoveries have been made in Lower Cretaceous basin deposits of the Gansu Province (China), notably the Lanzhou-Minhe Basin and the Jiuquan area. In the Lanzhou-Minhe Basin, which is located in the border area between Qinghai Province and the central part of Gansu Province, diverse and well-preserved assemblages of dinosaur (theropod, sauropod, and ornithopod), pterosaur, and bird tracks were discovered (Zhang et al., 2006), along with ornithopod (You et al., 2005a) and sauropod skeletal fossils (You et al., 2006). The Jiuquan area of northwestern Gansu Province is located in the middle of the Altun Mountains, the Qilian Mountains, and Mazongshan (Beishan). During the Early Cretaceous, numerous sedimentary basins were formed in the Jiuquan area, including the Changma, Hanxia, Jiuxi, and Beishan basins. All are mainly composed of terrestrial clastic sediments with reddish oxidation colors ("red beds"), which indicate an arid and fully terrestrial environment (Peng et al., 2011).

In the Lower Cretaceous deposits of the Jiuquan area, abundant non-avian dinosaur and bird fossils have been discovered thus far, including the tyrannosaurid *Xiongguanlong* (Li et al., 2010), the ornithomimid *Beishanlong* (Makovicky et al., 2010), the troodontids cf. *Harpymimus* (Barsbold and Perle, 1984) and *Sinornithoides* sp. (Russell and Dong, 1993), the therizinosaurid *Suzhousaurus* (Li et al., 2007), the titanosauriform sauropods *Gobititan* (You et al., 2003) and *Qiaowanlong* (You and Li, 2009a), the iguanodontid ornithopods *Jintasaurus* (You and Li, 2009b) and *Xuwulong* (You et al., 2011), the psittacosaurian *Psittacosaurus* (Xu, 1997), the neoceratopsians *Archaeoceratops* (Dong and Azuma, 1997) and *Auroraceratops* (You et al., 2005b), and numerous

CONTACT Lida Xing xinglida@gmail.com School of the Earth Sciences and Resources, China University of Geosciences, Beijing, China.

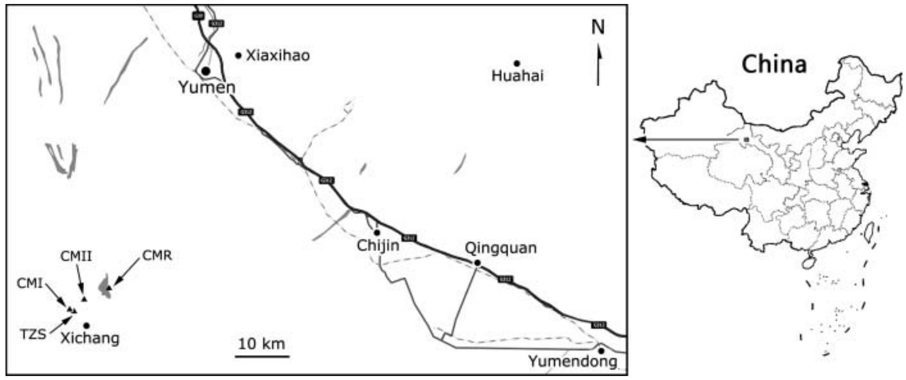

Figure 1. Geographic map showing the location (triangle icon) of the Changma dinosaur tracksites in Changma Township, Yumen City, Jiuquan area, northwestern Gansu Province, China. CM I, CM II = Changma tracksites I–II, CMR = Changma reservoir tracksite, TZS = Tuzhashan tracksite. Lines at upper left are rivers.

ornithuromorph and enantiornithid birds, such as *Gansus, Yumenornis, Changmaornis*, and *Jiuquanornis* (Wang et al., 2013). Generally, the dinosaur and possible bird faunas from the north Qilian–Beishan area are more derived than those of the Jehol Biota (Tang et al., 2001).

In the Changma Basin, in the 1990s and 2000s, geologists sporadically discovered tetrapod tracks, including an isolated ornithopod track and several bird tracks from a site (Tuzhashan tracksite) near Tuzhashan (personal observation by Cuo Peng, Geological Museum of Gansu) (Fig. 1). The former is in the Gansu Provincial Museum, whereas the latter have been lost. In 2013–2014, the senior author discovered three new tracksites (Changma tracksite I, II, and Changma reservoir tracksite) in the Changma Basin with ornithopod and sauropod tracks preserved as impressions (molds), and shallow and deep three-dimensional natural track casts. Here, we describe these new tracks in detail and provide an interpretative model for the formation of deep natural track casts and associated foot pathways in soft substrate.

Geological setting

Xiagou and Zhonggou formations

The tracks described herein were all discovered in the Changma Basin, in the northwesternmost corner of the Qilian Mountains, where a relatively continuous and complete sequence of Lower Cretaceous strata is well exposed (Peng et al., 2011). Niu (1987) divided the strata of the North Qilian–Beishan area (from bottom up) into the Chijinqiao, Chijinbao, and Xinminbao formations. In 1989, the Gansu Bureau of Geology and Mineral Resources divided the strata into the Chijinqiao, Xiagou, and Zhonggou formations. Later, Peng (2012) divided them into the Chijinqiao, Chijinbao, Xiagou, and Zhonggou formations (Fig. 2), and this is followed here. Peng (2012) assumed a Berriasian–Barremian age for the Chijinqiao and Chijinbao formations, and a Barremian–Albian age for the Xiagou and Zhonggou formations, based on the records of invertebrate fossils, such as bivalves, conchostracans, and ostracodes, whereas other authors have proposed an Early Aptian age for the Xiagou Formation based on the records of vertebrate fossils (You et al., 2005c; Harris et al., 2006; Lamanna et al., 2006; Suarez et al., 2013).

The sediments of the Zhonggou Formation (late Early Cretaceous in age) of the Changma area, consist of brownish red and purple-red conglomerates, medium-grained sandstones, siltstones, and fine-grained sandstones. The depositional environment has been interpreted as a meandering river (Peng et al., 2011; Peng, 2012).

The sediments of the Xiagou Formation (middle Early Cretaceous in age) below consist of grayish to yellow, fine-grained sandstones, thick-bedded calcareous siltstones, silty mudstones, and a thick-layer of gray mudstone on top (fining upward sequence). This sedimentary sequence possibly indicates a depositional environment changing from a fluvial delta plain to a shallow lacustrine shore and back to a fluvial delta plain (Peng et al., 2011; Peng, 2012).

Invertebrate traces and paleoecology of the Xiagou Formation

There are numerous invertebrate trace fossils in the unit below the track layer of the Changma reservoir tracksite (Fig. 3). Although a detailed study of the invertebrate trace fossils is beyond the scope of this work, two outstanding ichnotaxa should be mentioned here because of their abundance and relative wide distribution.

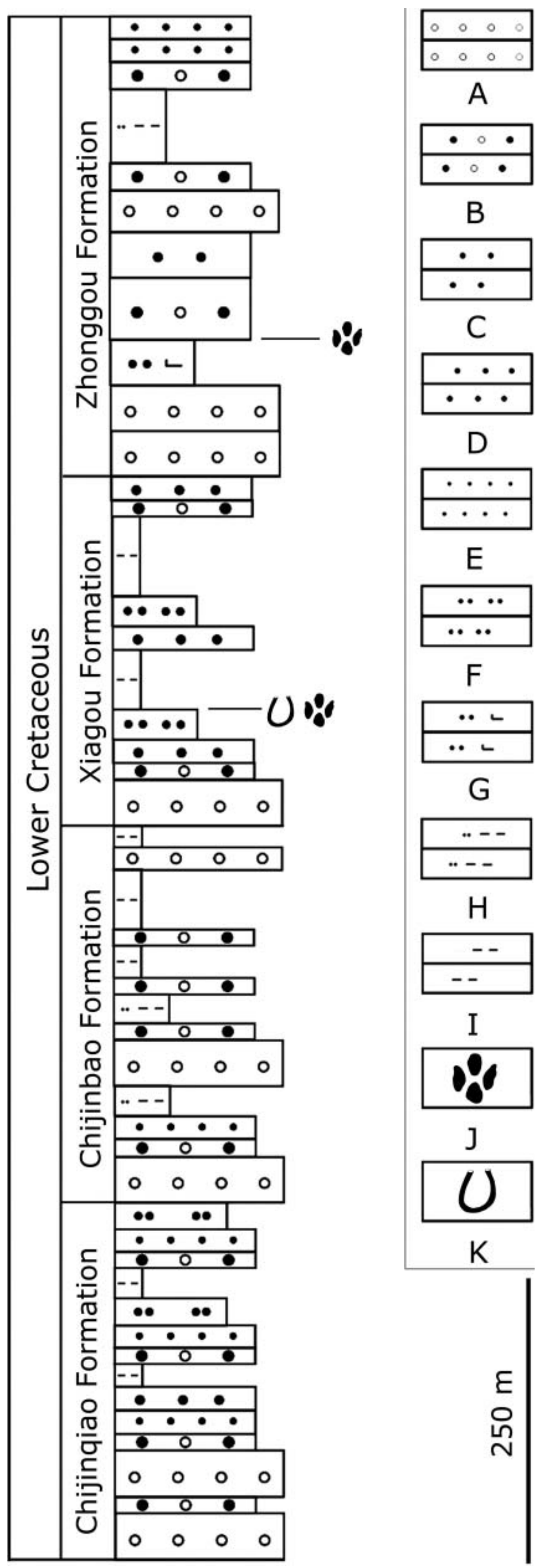

Figure 2. Stratigraphic column of the Lower Cretaceous strata of the Changma area (emended from Peng et al., 2011). **A.** Fine-grained conglomerate. **B.** Calciferous coarse-grained sandstone. **C.** Coarse-grained sandstone. **D.** Medium-grained sandstone. **E.** Fine-grained sandstone **F.** Siltstone. **G.** Calcareous siltstone. **H.** Silty mudstone. **I.** Mudstone. **J.** Dinosaur tracks. **K.** Invertebrate traces.

The first notable ichnotaxon is preserved as straight, slit-like burrows with high density on an upper bedding plane. The burrows are preserved in negative epirelief, ca. 20 mm in length and 2 mm in width. The density of the burrows has been estimated to be in the range of 700 to 900 specimens per square meter, and the orientation of the burrows appears to be random. The burrows are passively filled with loose sediment, which commonly weathers out to leave the burrows empty. Vertical sections reveal a U-shaped burrow outline as well as a weakly developed spreite, which allows an assignment of these burrows to *Diplocraterion parallelum* (Fig. 3A,B,D).

In the siltstone and mudstone above that sandstone layer, as well as at the base of another sandstone layer, cylindrical and straight to slightly curved burrows occur preserved in endorelief and in positive hyporelief. These burrows are also densely packed with estimated up to 300–500 specimens per square meter. The probably actively sand-filled burrows nicely weathered out from the fine-grained host rock and show a rough surface, although no ornamentation or lining is visible in the studied material. They are traceable over a distance of 70 mm and their diameter varies between 3 and 5 mm. Branching is absent and orientation seems to be random. Therefore, these burrows are assigned to *Planolites montanus* (Fig. 3C,D).

The documented layers with invertebrate bioturbation indicate sporadic and rapid colonization of substrates as soon as favorable conditions were given for endobenthic life in an otherwise hostile paleoenvironment. In the given geological setting with predominantly continental depositional environments, such colonization windows generally indicate infrequent marginal-marine incursions because mass occurrences of *D. parallelum* are commonly related to marginal-marine environments such as tidal settings and estuaries (e.g., bars and sand flats; Goldring, 1962; Frey and Goldring, 1992; Bromley and Hanken, 1991; Bann and Fielding, 2004). However, the deposits of the Xiagou Formation where the traces were found show no indications for marine influences by sedimentary features or fossil remain thus far (Trewin and McNamara, 1995; Kim and Paik, 1997; Peng, 2012). Therefore, a more comprehensive future study of the depositional environment might help to clear this contradiction. *P. montanus* is a generalist trace fossil with a wide distribution from continental to deep-marine settings. However, its dense occurrence in monoichnospecific assemblages as the one described here is typically related to stressed environments such as reduced salinity as brackish-water environments (Knaust and Costamagnam, 2012). The described *P. montanus* is somehow comparable to the original material described by Richter

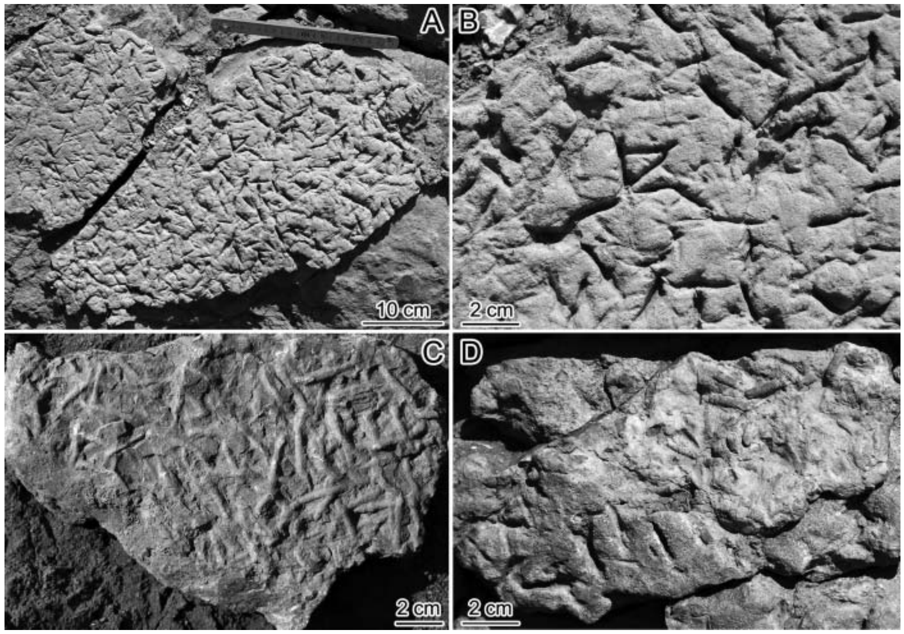

Figure 3. Photographs of invertebrate traces from the Changma reservoir tracksite. **A-B**. *Diplocraterion parallelum*. **C**. *Planolites montanus*. **D**. *Planolites montanus* above *Diplocraterion parallelum*.

(1937) from Upper Carboniferous paralic mudstones of western Germany.

Tracksites and material (see map in Fig. 1 for overview)

1) Changma tracksite I (GPS: 39°52′50.81′N, 96°43′28.81″E) of Changma Township, Yumen City, Jiuquan area, northwestern Gansu Province, China (Fig. 4). The slope of the rock surface is about 60°. Tracks are preserved in grayish-yellow fine sandstone from the Lower Cretaceous Xiagou Formation. The material consists of two isolated ornithopod tracks, of which the better preserved one is deposited in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China under specimen numbers IVPP V20274.

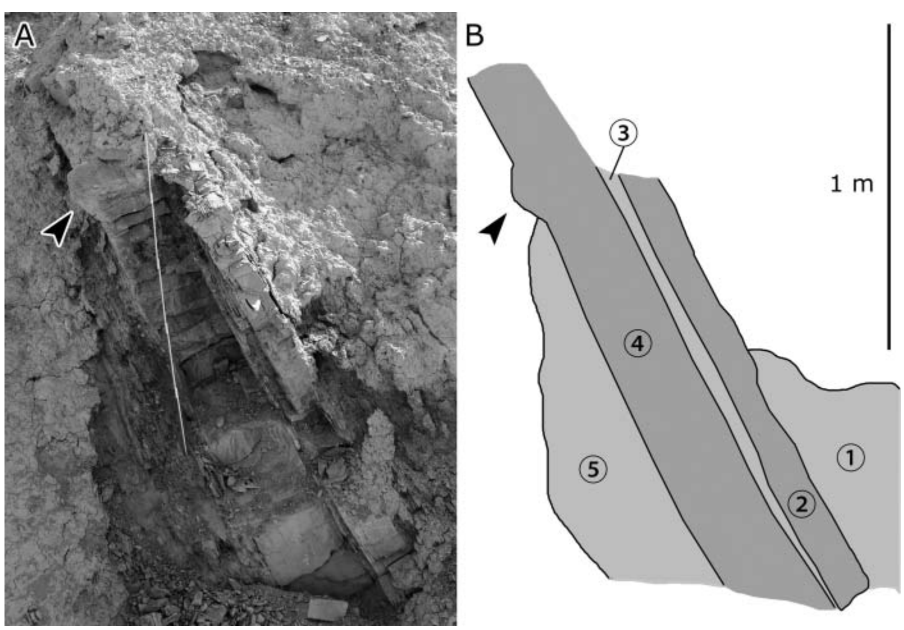

Figure 4. Overview photograph (**A**) and sketch of outcrop (**B**) of the Changma tracksite I, Gansu Province, China. The arrow shows an incomplete, natural dinosaur track cast, of probable ornithopod origin. 1, 3, 5 = mudstones; 2, 4 = fine-grained sandstones.

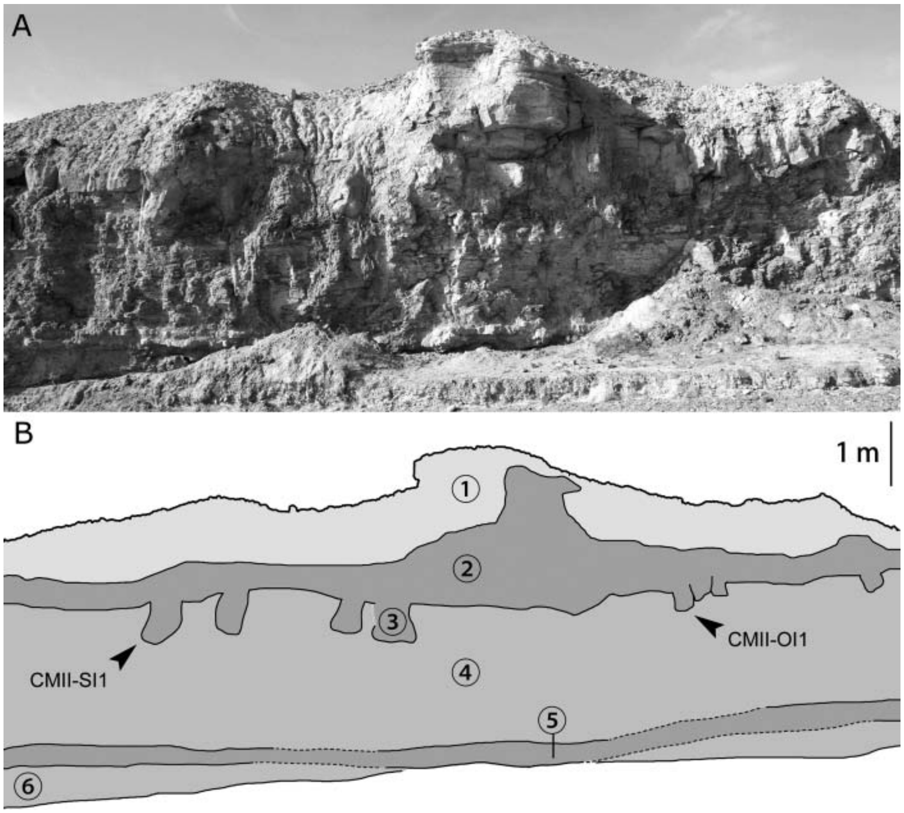

Figure 5. Overview photograph (A) and sketch of outcrop (B) of the Changma tracksite II, Gansu Province, China with position of sauropod deep natural cast (CMII-SI1) and ornithopod deep natural cast (CMII-OI1). 1 D sandy recent soil formation; 2, 5 D fine sandstones; 3 D deep natural dinosaur track cast of probable sauropod origin; 4, 6 D mudstones.

2) Changma tracksite II (GPS: 39°54′5.44″N, 96°45′24.39″E) of Changma Township (Fig. 5–7). It is located in an exposure of the Xiagou Formation in the Changma area characterized by a typical sandstone–mudstone intercalation, indicating a distributary channel and interdistributary bay depositional environment.

Tracks are preserved in grayish yellow fine sandstone of the Xiagou Formation. At least eight deep tracks recording three-dimensional foot movement were discovered,

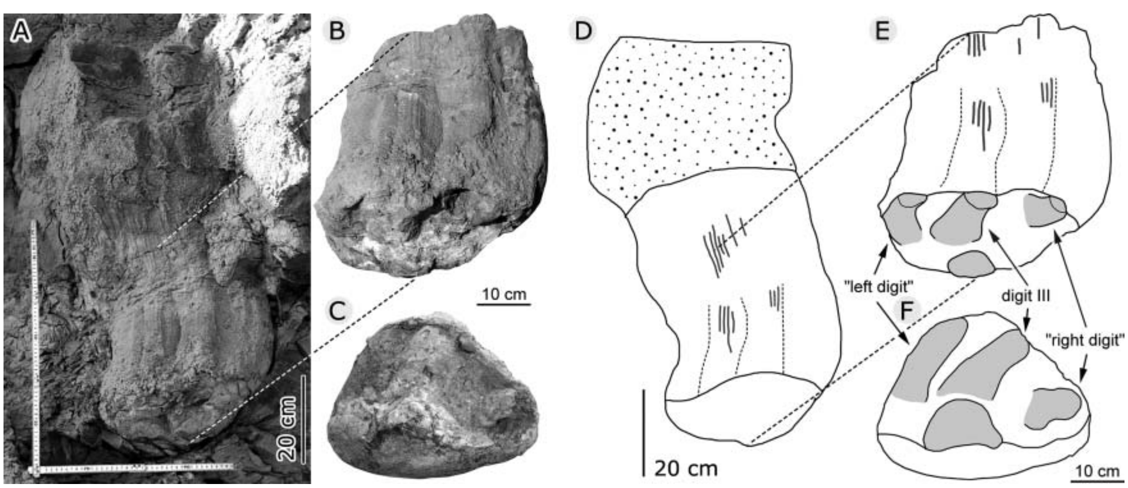

Figure 6. Deep natural ornithopod track cast with pronounced, vertical striation marks, CMII-OI1. A. Photograph of the cast *in situ*. B. Collected specimen, with the mudstone in the lower surface of the track removed and digits exposed. C. Lower surface of the track with three digit and heel impressions clearly visible. D–F. Interpretative outline drawings with the same orientation as for the photographs shown in A–C, respectively. The slightly bent shape of the casts indicates a certain degree of horizontal movement during foot fall and/or foot removal.

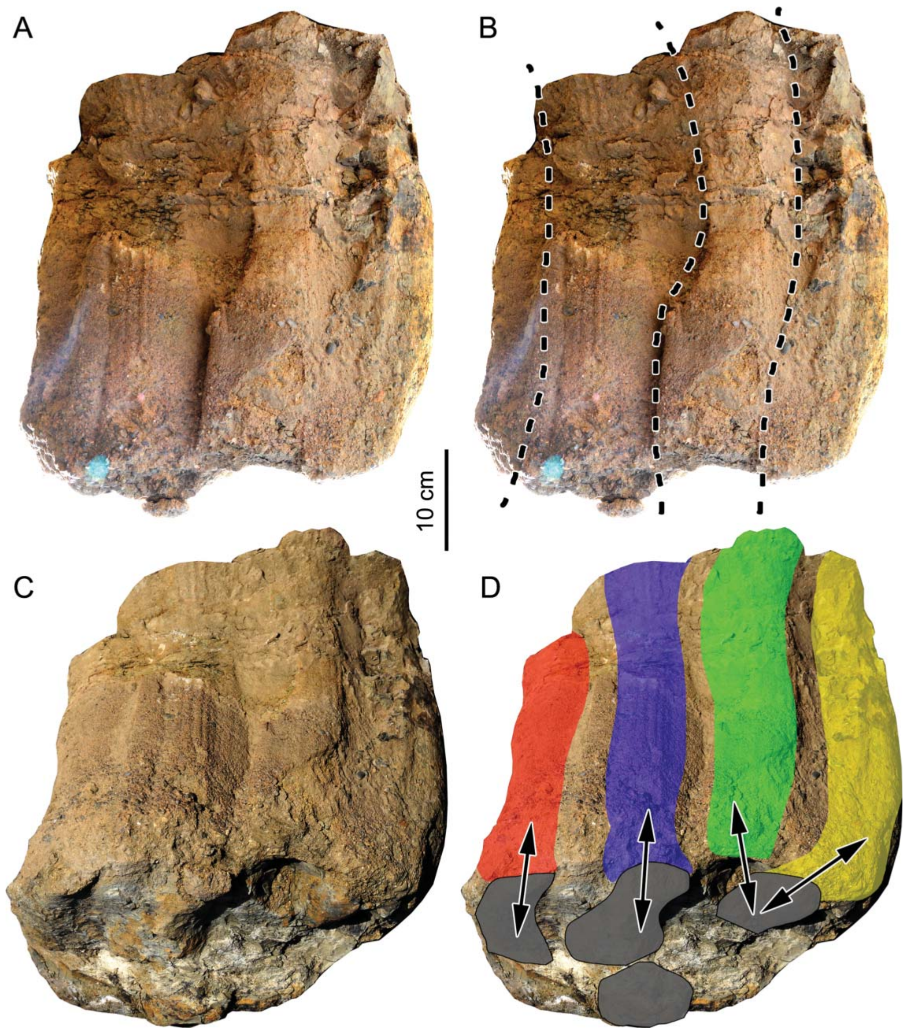

Figure 7. Photograph of deep natural ornithopod track cast CMII-OI1. **A**. Anterior view. **B**. Dashed lines indicate the deepest part of the three grooves that separate three well-marked ridges (coloured in D). **C**. Anterior view. **D**. The left ridge is connected with the "left" digit, the second from left ridge with the middle digit III, and the third from left and right ridge are both connected with the "right" digit. The red and blue ridges are interpreted as exit traces, whereas the green and yellow ridge are interpreted as entry (yellow) and exit (green) traces, respectively, for the "right" digit. Note that all three digits are rotated to the right side.

including those of ornithopods and sauropods. Lida Xing and Lu Li collected the two best preserved tracks, which are currently deposited in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. Two deep natural track casts are cataloged as CMII-OI1 and CMII-SI1m–1p.

3) Changma reservoir tracksite (GPS: 39°55′33.22″N, 96°49′14.61″E) of Changma Township. Two poorly preserved ornithopod trackways arepreserved in the fine-grained, grayish-yellow sandstone of the Xiagou Formation. The slope of the tracksite is about 45°. A trackway and one isolated track are cataloged as CMR-O1 and CMR-OI1, respectively. All tracks are *in situ*.
4) Tuzhashan tracksite (GPS: 39°52′45.73″N, 96°43′51.95″E) of Changma Township. A single isolated ornithopod track (TZS-OI1) is preserved in grayish, thick-bedded, calcareous siltstone of the Zhonggou Formation.

Methodology

Photogrammetric models were produced for selected tracks using Agisoft Photoscan Professional from multiple digital photographs taken with a Canon EOS 5D Mark III, and converted into scaled, three-dimensional, textured mesh models. The mesh models were then imported into Cloud Compare, where the models were rendered with scaled color topographic profiles.

For the description of the natural track casts, we follow the terminology that Xing et al. (2015) has recently proposed:

Length: the maximum length of the track casts.

Width: the maximum width of the track casts.

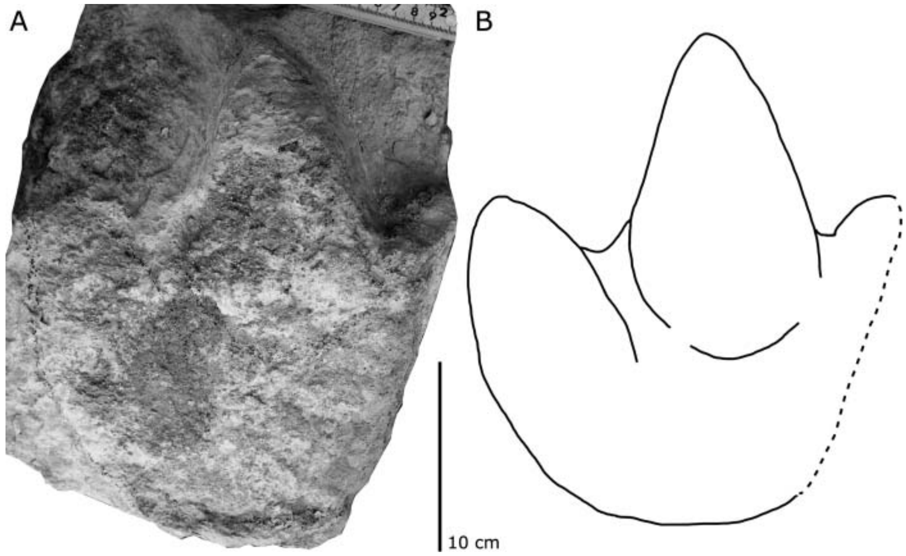

Figure 8. Photograph (**A**) and interpretative outline drawing (**B**) of a shallow ornithopod natural track cast, IVPP V20274.

Figure 9. Overview photograph (**A**) and interpretative outline drawing (**B**) of the Changma reservoir tracksite, Gansu Province, China. There is evidence for a trackway of a large tridactyl—possibly ornithopod—dinosaur (CMR-O1).

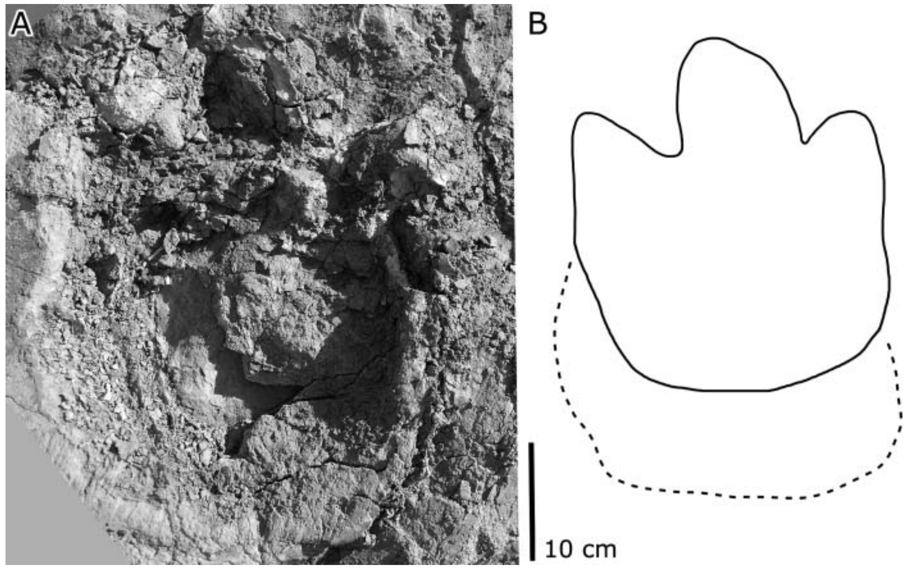

Figure 10. Photograph (**A**) and interpretative outline drawing (**B**) of an ornithopod track (impression), CMI-OI1.

Depth: the vertical distance between the upper and lower surface of the natural track cast; we distinguish between upper and lower surface considering their different size, with the upper surface often being smaller than the lower surface due to substrate collapse after foot withdrawal; the lower surface may correspond to the true dimensions of the trackmaker's foot, if not considerably affected by foot kinematics (e.g., varying angle during inserting and pulling out of the foot).

Striations (entry and exit): on lateral or medial sides of the track and perpendicular to the sole surface, often parallel to each other; mostly caused by skin texture and/or unguals.

Ornithopod tracks

Deep natural track casts

Description

One isolated, deep natural track cast from CMII cataloged as CMII-OI1 was *in situ* being 57 cm in total depth and 22 cm in length (Fig. 6; Table 1). However, due to breakage during the excavation, only the lower 37 cm of the track could finally be recovered. The track cast is oval in shape and exhibits pronounced vertical striation marks, three distinct digits, and a heel (metatarsophalangeal pad) impression on the lower surface (Fig. 7). The middle digit III is the widest. The outer digits cannot be numbered with certainty, but the "left" digit is longer compared with the "right" digit which is shortest (in anterior view that is shown in Fig. 7D). Digit III and the "left" digit are basically parallel, with a length of 18 cm. Only the distal portion of the "right" digit is exposed, which is approximately 14.5 cm in length. The metatarsophalangeal pad is round and more deeply impressed than all three digits. On the lower surface, the divarication angle between the "right" digit and digit III is 43°, and the divarication angle between the "left" digit and digit III is 28°. Narrow, closely spaced, parallel, vertical striation marks, 8–10 mm in width are visible on the lateral side of the cast above digit III and the "right" digit. The anterior part of the track cast is well preserved and four well-marked, parallel, vertical, slightly sinuous ridges, separated by three grooves both ranging from the top to the bottom of the cast are visible (Fig. 7). At the bottom, these ridges and grooves connected with the three digits and "interdigital notches," respectively (Fig. 7D).

Interpretation

The presence of three digits and, notably, the well-marked, round metatarsophalangeal pad indicate that this track is a deep ornithopod rather than a theropod natural track cast. The overall shape of deep sauropod *manus* natural track casts may sometimes look similar, but these casts never show three separated digit impressions and pronounced ridges, and grooves in the anterior part are generally absent or not so well developed. Contrary to shallow ornithopod natural track casts, in deeply impressed specimens mostly the lateral surfaces are well preserved, showing details such as ridges and grooves or striation marks while the preservation of the lower surface is poor and lacks substantial details of the digits and metatarsophalangeal pads (see also Xing et al., 2011, plate I).

Deep natural track casts offer insight into the locomotor dynamics of the trackmaker, notably footfall, weight-bearing, and kick-off phases of the step cycle (Avanzini et al., 2011; Xing et al., 2012). In the present case, three grooves separate the track casts into four ridges (Fig. 7) and these correspond to the digits and "interdigital notches," respectively. They are interpreted as entry and exit traces (pathways) of the three digits. However, the presence of three grooves and four ridges implies that there are not only coincident exit and entry foot pathways, but that there is at least one additional, separated entry or exit pathway corresponding to one of the digits. The width of the four ridges is equal to or slightly larger than that of the distal ends of the digits II to IV. In the view of Fig. 7D, the two ridges from the left side are each well connected with the left digit and the central digit III impressions, and they are interpreted as "digit pathways" having been formed by the digit and notably ungual during the withdrawal of the foot associated with a slight forward drag of the digits resulting in ridges and grooves (see also McCrea et al., 2014). The two remaining ridges at the right side are both connected with the "right" digit, and this suggests one entry ridge and one exit ridge for this digit. Of course, other interpretations for possible digit pathways cannot be excluded, but we assume that the possibility that exit ridges (traces) are preserved is higher than the preservation of entry ridges (traces), because the former may potentially overprint/obscure the entry ridges (traces).

Because all three digits preserved on the lower surface of the cast are turned outward, it is assumed that at this final depth the foot movement into the substrate was decelerated and stopped due to the presence of a firm layer, resulting in a pronounced outward rotation of the digits and the preservation of distinct digit and heel pad traces. This also implies that a thick (about 60 cm) layer of soft substrate was located on top of a firm layer. Similar preservation scenarios (firm layer below a thick layer of soft substrate) were also deduced by tracks from the Late Jurassic of NW Switzerland (Marty, 2008), and by recent human footprints left in thick layers of soft substrate covered with a layer of microbial mats (Marty et al., 2009). These examples document that the foot movement is decelerated by the presence of an underlying firm layer rather than simple compaction of "an infinite" layer of soft substrate.

In the Changma specimen, the "left" digit and digit III fully contacted the top of the firm layer at the bottom of the track, while only the distal end of the "right" digit touched this. The metatarsophalangeal pad was most deeply impressed. Afterwards, the foot was pulled out from the sediment, and while it was not withdrawn completely vertical, the "right" digit left an additional ridge (exit trace) in contact with the surrounding substrate. In contrast, many other ornithopod natural track casts document that during the final part of the load-bearing phase, the foot was lifted more vertically out of the track, while the toes were held in a way where they did not contact the surrounding substrate (Xing et al., 2012). This is suggested by the lack of further exit traces (dirges). An alternative functional explanation is that digits might have been contracted showing decreasing divarication while being pulled out of the sediment.

It is worth mentioning that Xing et al. (2012) described a deep hadrosauriform natural track cast (QJGM-C1) from the Lower Cretaceous Lotus tracksite in Chongqing Municipality, south-central China and assigned it to *Caririchnium lotus*. This cast is 37.1 cm deep and has well-preserved anterior and lateral views. Dragging traces of the digits on the surface of QJGM-C1 demonstrate modifications in foot posture (extension and increased divarication angle between the digits) that took place during footfall. These modifications presumably increased stability and load-bearing in response to ongoing compaction of an initially unconsolidated, soft substrate.

The striation marks on CMII-OI could either have been caused by tubercles or scales (Difley and Ekdale, 2002) or they could also be traces that formed when the distal edge of the ungual dragged through the substrate. Irregularities on the hoof of a modern bovine commonly produce slip traces in moist mud, and complex (intersecting) patterns of parallel striation marks on track casts can demonstrate the footfall and pull out process of the *pes* (Difley and Ekdale, 2002). However, only in the two middle ridges (Fig. 6) of CMII-OI1 distinct striations are preserved, while almost no striations are observed in the outer ridges.

The flexibility of the *pes* digits of ornithopods has been discussed based on the tracks of hadrosauriforms (Moreno et al., 2007). According to Moreno et al. (2007), the tracks of hadrosauriforms show a high inflexibility of their toes. Because the Changma specimens cannot be specified and attributed to a distinct ornithopod group, we cannot test this here. Nevertheless, the deep casts we document here give significant insights into the *pes* movement of these dinosaurs, providing functional information that might supplement those known from the skeletons.

Impressions and shallow natural track casts

Description

Two natural track casts were found at the Changma I tracksite (Fig. 4). These track casts are preserved in fine-grained, grayish sandstone. IVPP V20274 (Fig. 8) is well-preserved and was collected, whereas the second track is only partially preserved and was left *in situ*. IVPP V20274 is tridactyl and the lateral

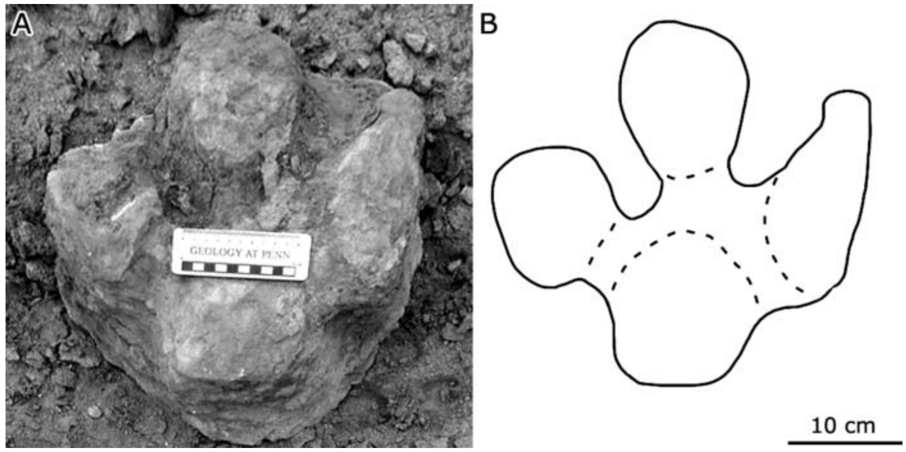

Figure 11. Overview photograph (**A**) and interpretative outline drawing (**B**) of a shallow, typical ornithopod natural track cast TZS-OI1 from the Tuzhashan tracksite, Gansu Province, China.

side of the outer digit is damaged. The middle digit is directed forward and is well developed. The length: width (L/W) ratio of the middle digit is 1.2. The L/W ratio of the anterior triangle is 0.41.

One trackway from the Changma reservoir tracksite was cataloged as CMR-O1 and consists of three consecutive tracks preserved as concave epirelief (Fig. 9). There is also an isolated track discovered near CMI-O1 and catalogued as CMI-OI1 (Fig. 10). All these tracks were already severely weathered and were left *in situ*. The CMR-O1 trackway has a pace angulation of ~160°. CMR-O1L1 is the best preserved track and has an inward rotation of ~13° and three recognizable digit impressions, of which digit III is only incompletely exposed. The walking direction of CMI-OI1 is consistent with that of CMR-O1. The L/W ratio of CMI-OI1 is 1.1, the L/W ratio of the anterior triangle is 0.27. The three digits of CMI-OI1 are recognizable, among which digit III is the longest and the two external digits II and IV are subequal in length.

One isolated but well-preserved natural track cast was discovered at the TZS site and is cataloged as TZS-OI1 (Fig. 11). The track is a subsymmetric *pes* trace, with quadripartite morphology consisting of impressions of three digits and a heel pad separated by pronounced ridges. A concrete determination and numbering of digits II and IV cannot be given. The "right" outer digit (based on Fig. 11) has a clear ungual trace. The distal portion of the "left" outer digit may be damaged. The L/W ratio is 1.0, and the L/W ratio of the anterior triangle is 0.30.

Interpretation

All impressions and shallow natural track casts are interpreted as ornithopod tracks, because they are very similar in overall shape to those that are frequently found in Lower Cretaceous strata of Gansu Province (such as Zhang et al., 2006, fig. 12; Xing et al., 2015, fig. 8). There are a number of ornithopod tracks known from the Yanguoxia tracksites in the Lanzhou-Minhe Basin, including four parallel ornithopod trackways and several natural casts (Zhang et al., 2006). One well-preserved ornithopod *pes* natural track cast from Yanguoxia tracksite No. 1 has an L/W ratio of 1.3 and a L/W ratio of the anterior triangle of 0.41 (Zhang et al., 2006, fig. 12). Another ornithopod natural track cast GDM-Y-SS1-1 from Yanguoxia SS1 tracksite, also has an L/W ratio of 1.3, and it shows a relatively strong mesaxony (the L/W ratio of the anterior triangle is 0.38) (Xing et al., 2015).

Compared to better preserved IVPP V20274 and CMI-OI1 tracks from the Xiagou Formation, TZS-OI1 from Zhonggou Formation has a lower L/W ratio (1.0 vs. 1.1–1.2) and a degree of mesaxony (0.30) that falls within the range of the former (0.27–0.41). Such similarities are not surprising or of much ichnotaxonomic use, because medium-sized ornithopod tracks from the Early Cretaceous are relatively conservative in foot morphology (Kim et al., 2009; Lockley et al., 2014). In addition, the L/W ratio is smaller (0.9), while the degree of mesaxony is rather weak (0.16).

In morphology, the ornithopod tracks from the Xiagou Formation of the Changma region are close to the natural track casts from Lanzhou Basin with a similar L/W ratio, degree of mesaxony, and a well-developed digit III, all of which are characteristic features of *Iguanodontipus* (Zhang et al., 2006). The tracks from the Zhonggou Formation have a visible quadripartite morphology, which is close to *Caririchnium lotus* from Lower Cretaceous Jiaguan Foemation, Chongqing (L/W ratio 1.2, degree of mesaxony 0.32) (Xing et al., 2007).

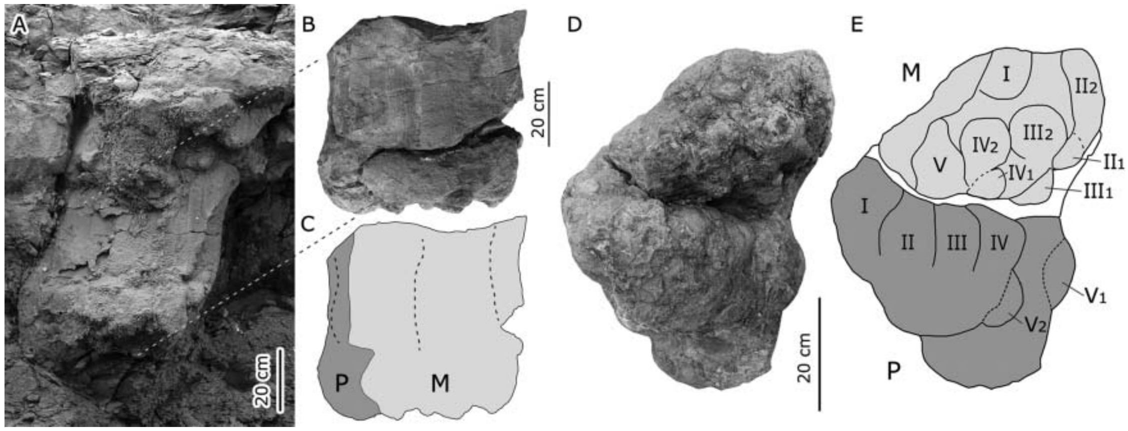

Figure 12. Deep sauropod natural track cast, CMII-SI1. **A**. Photograph of the track cast *in situ*. **B**. collected specimen, with the mudstone in the lower surface of the track removed and digits exposed. **C**. interpretative outline drawing corresponding to the view in B. **D**. lower surface of the track cast. **E**. interpretative outline drawing for D. M = manus, P = pes.

Deep sauropod natural track casts

Description

A single isolated deep sauropod natural track cast was discovered at Changma tracksite II and cataloged as CMII-SI1 (Figs. 12 and 13). Actually, CMII-SI1 is composed of two tracks, a left *pes* (= CMII-SI1p) and *manus* (= CMII-SI1m) track and *in situ*, which was at least 72 cm in depth and 57 cm in length (Fig. 12A–C). However, due to breaking during the collection process, only the lower 60 cm could be recovered. The lower surface of CMII-OI1 is well preserved, with distinct impressions of digits and metatarsophalangeal pads on both *pes* and *manus* (Fig. 12D,E).

CMII-SI1p is a *pes* natural track cast with a length/width ratio of 1.2 and with all five digits preserved. The claw marks of digits I–IV are indistinct. Digits II–IV are almost parallel. The digit IV trace is smaller than digits I–III. Digit V trace (numbered V2) is rather small, only half the size of digit IV. It is located adjacent to the lateral side of digit IV, and was possibly made by a foot callosity. There is another digit V trace (numbered V1) visible in a relatively lower surface (with a height difference of 15 cm) and a size inconsistent with that of digit V2, indicating that the *pes* was possibly sliding inwards (with respect to the direction of travel) and downwards (Fig. 14). The metatarso-phalangeal region is smoothly curved. Digit I has a visible ridge, which shows the sliding process of the digit, first perpendicular to the lower surface, gradually transitioning until about 40° between the lower surface and vertical of the cast. There are about 15 striation marks on the ridge, each approximately 10 mm in width.

The *manus* natural track cast CMII-SI1m is oval-shaped with a distinct outward rotation. Its length/width ratio is 0.6. It is well preserved and has rounded digits labeled I, II2, III2, IV2, and V. Similar to CMII-SI1p, in the lower surface, CMII-SI1m also (with a height difference of 15 cm) has digits II1–IV1, of which digit III1 is slightly lower (deeper in the substrate), while the other two digits are located at the same depth. The anterior view shows the ridges of digits I, II, and V very well. The ridge of digit V has about eight narrow, closely-spaced, parallel, and vertical striation marks, each 10 mm in width. The lateral view also exhibits that digit III has about six narrow, closely-spaced, and parallel striation marks, each 8–10 mm in width.

Interpretation

The length:width ratio of CMII-SI1m and CMII-SI1p (0.6 and 1.2, respectively) and the morphology of the digits are typical of sauropod tracks, such as tracks from the Lower Cretaceous Zhaojue tracksite (Feitianshan Formation, Sichuan Province) attributed to *Brontopodus* (Xing et al., 2014), or tracks from the Lower Cretaceous Jishan tracksite (Tianjialou Formation, Shandong Province) attributed to *Brontopodus/Parabrontopodus* (Xing et al., 2013).

Brontopodus (Farlow et al., 1989) is one of the most common and well-known Cretaceous sauropod track types. Previously, most Early Cretaceous sauropod tracks in East Asia have been attributed to either the wide-gauge *Brontopodus* (Lockley et al., 2002) or narrow gauge *Parabrontopodus* ichnogenera (Xing et al., 2013). CMII-SI1 is an isolated *pes–manus* track pair, most similar to *Brontopodus* based on the following features: U-shaped *manus* tracks, *pes* tracks longer than wide with large, outwardly directed claw marks on digits I–III, a small trace of digit IV, and a small callosity or pad mark representing digit V. The ratio of *manus* to *pes* size in CMII-SI1 is 1:1.7, which is larger than that of the Early Cretaceous

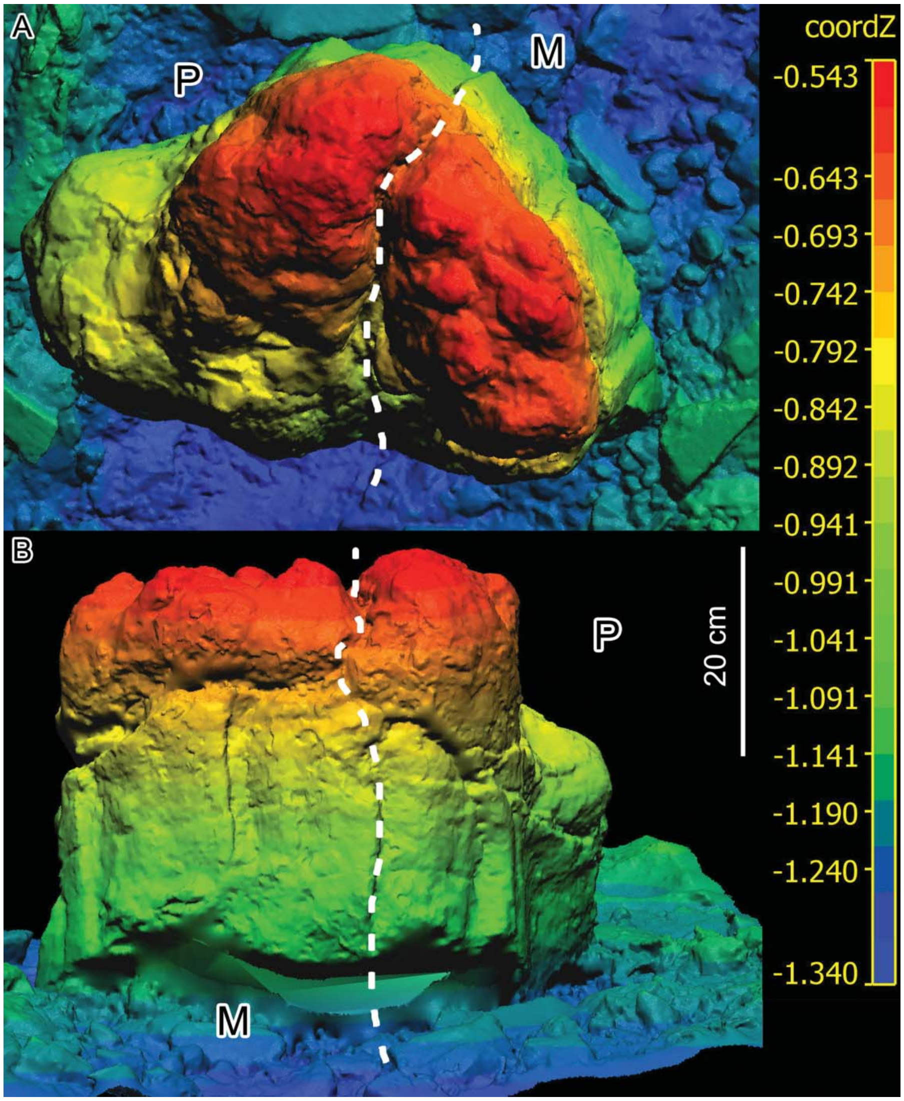

Figure 13. Photogrammetry of the 3D model of deep sauropod natural track cast, CMII-SI. **A**. The lower surface of the track cast. **B**. Lateral view of the track cast. M = manus, P = pes. Dashed line: the boundary between the pes and manus traces. The numbers in the right side: topographic profile scales (in meters).

ichnogenus *Brontopodus* from Texas (with a high heteropody of 1:3) (Farlow et al., 1989; Lockley et al., 1994) and closer to that of the Middle Jurassic *Polyonyx* (1:2) (Santos et al., 2009). However, some Chinese *Brontopodus* tracks, for example the Jishan *Brontopodus* tracks, also have a weak heteropody (1:1.5). Therefore, CMII-SI1 is tentatively assigned to *Brontopodus*, and the tracks were most likely left by titanosauriform dinosaurs of which skeletal fossils were discovered in the region (You et al., 2003).

Natural casts of deep sauropod tracks (three-dimensional tracks, preserved in convex hyporelief) are not rare (e.g., Milàn et al., 2005; Platt and Hasiotis, 2006; Mateus and Milàn, 2008; Romano and White, 2012), and they are generally exposed in vertical sections and not as track impressions on bedding planes (surfaces) (e.g., Lockley, 1997; Romano and Whyte, 2012). For this reason, they cannot always be studied three-dimensionally in the outcrop unless they are excavated and recovered. Also, they are generally not associated with any trackway (data).

On its lower surface, CMII-SI1 preserves fine details of the digits and some of the digit impressions are doubled. During step-cycle, first the *pes* and *manus* of the sauropod trackmaker decelerated and stopped within the soft substrate at a depth of about 55 cm, where II1–IV1 of the *manus* and V1 of the *pes* were preserved (Fig. 12). Then, the foot slid outwards and an additional 15 cm deeper into the soft substrate. Finally, this movement was stopped again (possibly because of the presence of a firm layer below) and additional digit impressions (digit I–IV and digit V2 in the *pes*; digit I, II2–IV2, V in the *manus*) were formed. The double digit impressions preserved on CMII-SI1p show that, in some cases, the foot was slipping within the substrate before a final stable

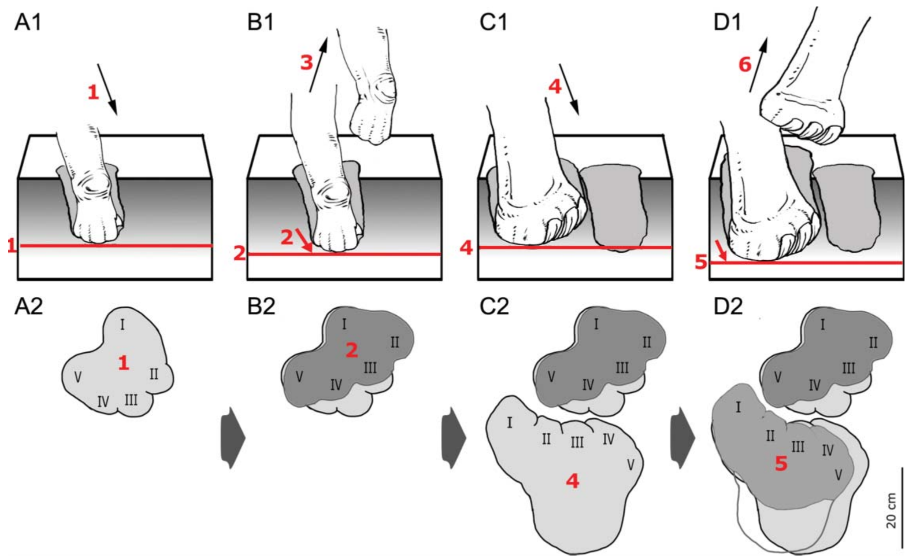

Figure 14. Schematic sketch showing a possible formation scenario for the deep, natural sauropod pes–manus track cast CMII-SI. **A1**. The forefoot (manus) penetrates into a thick layer of soft substrate until that compression of the substrate provides enough stability. **B1**. Due to substrate instability, the forefoot is sliding further down before it is pulled out of the deep track, eventually producing vertical striation marks in the anterior part of the track. **C1**. The hindfoot (pes) penetrates the substrate just behind the manus until that compression of the substrate provides enough stability. **D1**. Due to substrate instability, the hindfoot is sliding further down and inwards before it is pulled out, eventually producing vertical striation marks in the anterior part of the track. **E**. Both tracks are filled in with fine-grained sand, leading to the formation of the deep track casts after lithification (diagenesis). The gradient gray, from the dark to the light indicates increasing stiffness of the soft substrate as it is compacted/compressed by the foot. **A2, B2, C2, D2** show the formation of the track (view of the bottom) corresponding to **A1, B1, C1, D1**.

Table 1. Measurements (in cm) of the dinosaur tracks and trackway from the Changma tracksites.

Catalogue Number	D	L	W	PL	SL	II–IV	M	L/W
IVPP V20274	5.0	26.0	21.5	—	—	64°	0.41	1.2
CMR-O1L1	7.0	35.0	30.0	110	268	—	—	1.2
CMR-O1R1	—	—	—	150	—	—	—	—
CMR-O1L2	5.0	—	30.0	—	—	—	—	—
CMR-OI1	8.0	32.0	30.0	—	—	53°	0.27	1.1
TZS-OI1	5.0	31.8	31.0	—	—	67°	0.30	1.0
CMII-OI1	57.0	22.0	25.5	—	—	71°	0.16	0.9
CMII-SI1m	70.0	19.5	31.7	—	—	—	—	0.6
CMII-SI1p	72.0	40.0	34.0	—	—	—	—	1.2

D: Depth; L: maximum length; W: maximum width; PL: Pace length; SL: Stride length; II-IV: angle between digits II and IV; M: mesaxony (length/width ratio for the anterior triangle); L/W: Maximum length/ Maximum width.

position was reached. Bonnan (2005) considered enlargement, mediolateral compression, and development of a sickle-like curvature to be characteristic for the first pedal ungual, and this morphology may have enhanced the ability of the *pes* to gain traction on various substrates.

The morphology of CMII-OI1m from the Changma Basin is close to sauropod *manus* natural track casts from the Lanzhou-Minhe Basin. For example, ZJGM-1 also has well-developed digits II-IV (Xing et al., 2015, fig. 4). This shows that, although the two basins are not of the same geological age (early Aptian vs. earlier than or equal to Aptian–Albian for Lanzhou-Minhe Basin, Peng, 2012), the *manus* morphology of the inferred titanosauriform trackmakers was similar.

Conclusions and perspectives

The new dinosaur footprint assemblage from Jiuquan area of Gansu Province supplements the known skeletal record from Lower Cretaceous strata of this region as well as similar ichnofaunas from the Lanzhou-Minhe locality in the same province. Trackmaker candidates are ornithopods (possibly iguanodontids) and titanosauriform sauropods. The preservation of the tracks as deep natural casts allows a reconstruction of three-dimensional foot dynamics into and out of the substrate, especially in the tracks of ornithopods, by showing a distinctly shaped imprint with concrete digit traces on the bottom and lateral ridges as well as entry and exit striations laterally and above. Additionally, double impressions of digits at different depths in the sauropod tracks document lateral and vertical sliding movements that exist only in considerably deep tracks. It would be of high interest to excavate an entire trackway composed of deep natural track casts in order to study the variability of individual imprints along a single trackway. This would permit conclusions about behavior and locomotion capabilities including the digit flexibility of trackmakers.

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